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A Study of Asymmetrical Growth from Stump  
Sections of *Quercus velutina*

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A Comparative Pollen Analysis of two Bogs  
within the Boundaries of the Late Wisconsin  
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These papers are contributions No. 106-109, respectively, from the botany laboratories of Butler University.

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into the exact north point as located by a compass placed at the center of the section. The earth was dug away from each stump sufficiently to expose the main spreading roots and their location was also noted on the graph for each section.

In preparation for the measurements, radii were located on the graphs without reference to the sections themselves. The radii were so placed as to give measurements of growth from a number of standpoints, e. g. (1) along radii which were vertically above the main spreading roots and along other radii which were between these roots; (2) along radii which if extended would intercept competing trees 7 inches or over in diameter and within a radius of 35 feet from the center of the stump and along other radii dividing the distance between such competing trees; (3) along radii which divided the up-hill and down-hill sides of the stump; (4) along radii on or near each of the cardinal points of the compass.

Measurements along each of these radii were made by use of a 7x magnifier and a ruler divided into half-millimeters. Measurements could be made accurately to the nearest quarter-millimeter.

## OBSERVATIONS AND RESULTS

While the four sections selected for analysis varied considerably in diameter the count of their year-rings in the laboratory showed all of them to be exactly the same age, viz. 120 years. The primary object in this study was a search for data having a bearing on the problem of unsymmetrical or eccentric growth. Hence, while the observations are of interest in other ways, only those data having a bearing on the primary purpose of the study will be given consideration in the present paper.

### RELATION OF UNSYMMETRICAL GROWTH TO POSITION OF ROOTS

Auchter (1) has shown that there is little lateral movement of salts in trees and Glock (3) has suggested that eccentric growth is influenced by root activity. Accordingly, growth was measured in each section along radii which centered vertically upon main spreading roots and along radii which came between these roots. The data are summarized in Table I where it will be seen that the average growth along radii vertically above the roots was in every case greater than that along radii vertically above the spaces between roots. The percentage of difference ranges from 5.5 to 15.6. Not all radii vertically above roots were greater in growth than all radii



vertically between roots but the greatest single radius in each section was above roots and the shortest single radius in each section was between roots. It is also true that all radii above roots are longer than the nearest radii to them which are between roots. The longest radii, i. e. those above roots, do not have every year's growth increment greater than the growth of the shortest radii (those between roots). For example, growth along the longest radius in section 38-2 was greater than that along the shortest radius in 88.3% of the years but was less than that along the shortest radius in 6.66% of the years. Data for other sections are given in table II. These data would seem to indicate either that other factors besides root-location are concerned or that root-location as a factor in determining unsymmetrical growth varies during the life span of the tree.

The percentage of years in which growth along radii vertically above roots is greater than that above the space between roots increases with the age of the tree for the majority of the radii in all of the sections studied. These data are summarized in table III. Analysis of the data for section 38-2 will serve to illustrate the point. Radius 6 which was vertically above a root exceeded radius 4 (which was vertically above the space between two roots) in growth in only 12.5 % of the first 40 years of its life, in only 32.5% during the middle 40 years, but in 82.5% of the years during the last third of its life. This would appear to indicate that the particular root concerned in this case developed in the later life of the tree, or at least, that its effectiveness in unsymmetrical growth was not apparent until later in life. Radius 3 was at no time very different from radius 2 though the total length of the former was approximately 7% greater than the latter. Radii 11 and 1 were similar in general behavior with the immediately preceeding two radii. Radii 5 and 9 show the striking effect of root position during the first 40 years of the life of the tree. All other sections showed a more uniform effect of the root position and one in which its effectiveness increased with the age of the tree.

This would seem to indicate that root-activity as a factor in unsymmetrical growth may begin in the early life of the tree and continuously increase in effectiveness throughout life (radius 9 vs. radius 10 in section 38-3, radius 4 vs. radius 5 in section 38-4; table III); it may begin in early life along other radii and decrease in effectiveness with increased age (radius 5 vs. radius 9 in section 38-2); it may begin in middle life and increase with added age (radius 8 vs.

radius 9 in section 38-5) ; it may not begin until late in the life of the tree (radius 12 vs. 13 in section 38-4 and radius 5 vs. radius 10 in section 38-5) ; or it may begin in middle life and decrease in later life (radius 1 vs. radius 3 in section 38-5). All of this becomes intelligible if we assume that the various main spreading roots develop at different ages in the life of the tree, or at least, become effective as factors in growth at different periods in the life of the tree.

#### COMPETITION AS A FACTOR IN UNSYMMETRICAL GROWTH

If root-position has any relation to unsymmetrical growth in the trunk of trees it might be assumed that competition with other trees would thereby register at least a part of whatever effect it might have. In order to determine whether competition has any demonstrable effect in the trees under study, radii were laid out on the sections in positions which were such that, if the radii were extended they would intercept competing trees. Diameters of competing trees varied from 7 to 27 inches and distances from stumps under study varied from 7 to 31 feet. Data are given in table IV. Measurements of growth along these contrasted radii seem to indicate that competition has nothing directly discernible to do with the asymmetrical growth exhibited by the trees under study. In table IV it will be observed that the average length of radii which would intercept competing trees (marked "Competition" in the table) is greater than the average length of radii which would not intercept competing trees in sections 38-4 and 38-5 but less in sections 38-2 and 38-3. These results do not necessarily indicate that competition is without effect. They do indicate that competition exerts no demonstrable independent effect when occurring in a complex or other variable factors.

#### RELATION OF SLOPE TO UNSYMMETRICAL GROWTH

Douglass (2) found that in western yellow pine slope was an important factor in unsymmetrical growth when it was such that it made water available earlier on one side of the tree than the other. Data bearing on the relation of slope to growth are summarized in table V where it will be noted that average growth is greatest on the "up-hill" side of the tree in three out of the four cases. The number of spreading roots occurring on each of the two sides is of importance in this connection and it is not possible to study one of



these factors to the entire exclusion of the other. It will be noted, however, that in two of the sections the number of such roots is the same on each side. In the other two cases the greatest growth is on the side of the tree with the larger number of roots. The conclusion to be reached in regard to slope is that variations in slope in this study give no dependable relation to unsymmetrical growth though there is some evidence that the up-hill side of the tree may be favored.

#### RELATION OF CARDINAL POINTS OF THE COMPASS TO UNSYMMETRICAL GROWTH

According to Lodewick (6) it is sometimes maintained that trees growing on a level site will show an eccentricity in diameter and that the south and west sides will have greater growth, though he did not find this to be true in his own study. The present study does not give a fair approach to this question because all of the trees under consideration were on slopes. The data in this connection are summarized in table VI where it will be seen that no consistent relation is apparent between the cardinal directions of the compass and amount of growth. Whatever the effect of direction may be, it is overshadowed by other factors in this study.

#### DISCUSSION

While the location of main spreading roots is the only factor showing any plainly demonstrable relation to unsymmetrical growth in this study it must not be assumed either that they are the only important factor or that all of the apparent relation is really due to root position alone. It is obvious that we are dealing with a number of factors, some known and others unknown, no one of which has been isolated. Our results are due, therefore, to a combination of factors, root-position being most readily measurable and of such magnitude in its effect as to overshadow and obscure the others.

In the very nature of the case, no account was possible to be taken of the relation between the position of long and short radii of growth and the location of branches and general crown coverage. Even in those studies which are carried on in such a manner as to be able to determine zonal differentiation in crown coverage it is not possible to demonstrate definite relationship with unsymmetrical growth because it is not possible to detect curved or twisted conducting units nor is our knowledge of zonal conduction of food sufficiently adequate to permit a basis for calculation of relationships.

The best we are able to do at present is to say that unsymmetrical growth is due to a combination of factors, some internal and some external of which location of roots, itself determined partly by internal and partly by external factors; variations in slope or other soil relations; and competition with other trees are the most likely.

## CONCLUSIONS

1. Measurements of wood growth were made along a number of radii on each of four sections cut from the tops of stumps of *Quercus velutina* each 120 years old and each showing marked unsymmetrical growth.

2. Average growth along radii vertically above main spreading roots is in every case greater than that along radii vertically above the spaces between such roots.

3. The percentage of years in which the radii above roots have growth for individual years greater than the growth along radii vertically between roots increases with age of the tree.

4. Competition exerts no demonstrable independent effect upon unsymmetrical growth when it occurs as a part of a complex of other variable factors.

5. Variations in slope gave no dependable relation to unsymmetrical growth though there is some evidence, in the case of two sections where the other major factor was equivalent, that the up-hill side of the tree is favored at the expense of the down-hill side.

6. The cardinal points of the compass yielded no demonstrable independent effect upon unsymmetrical growth when occurring as a part of a complex of other variable factors.

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TABLE I

Relation between growth along radii which center on main spreading roots and those which come between such roots. Figures are averages of all radii of each type for each section.

Section	Radii on Roots		Radii between Roots	
	Number of radii	Growth	Number of radii	Growth
38-2	4	301.81 mm.	3	286.15 mm.
38-3	4	386.50	5	352.40
38-4	10	291.25	3	254.25
38-5	3	378.83	5	327.60

TABLE II

Showing relation of growth along longest and shortest radii of each section throughout the 120 year period.

Section	Percentage of years in which		
	Growth along longest radius is greater than along shortest radius	Growth along longest radius is the same as along shortest radius	Growth along longest radius is less than along shortest radius
38-2	88.30%	4.998%	6.664%
38-3	66.64	17.493	16.66
38-4	79.968	14.994	4.998
38-5	51.646	18.32	29.988

TABLE III

Showing relation of effectiveness of root-position in unsymmetrical growth to life-period of the tree.

Section	Radii on vs. radii between spreading roots	Percentage of years in which growth on radii vertically above roots is greater than adjoining radii between roots		
		First 40 years of life of tree	Second 40 years of life of tree	Third 40 years of life of tree
38-2	6 vs. 4	12.5%	32.5%	82.5%
	3 vs. 2	40.0	53.5	50.2
	11 vs. 1	32.5	40.0	55.5
	5 vs. 9	67.5	57.5	27.5
38-3	9 vs. 10	62.5	85.0	65.0
	8 vs. 2	27.5	60.0	65.0
	4 vs. 1	42.5	67.5	75.0
38-4	8 vs. 5	7.5	55.0	77.5
	4 vs. 5	62.5	100.0	90.0
	12 vs. 13	46.5	45.0	87.5
	10 vs. 11	22.0	20.0	70.0
38-5	5 vs. 10	37.5	17.5	60.0
	1 vs. 3	35.0	82.5	50.0
	8 vs. 9	10.0	62.5	85.0



TABLE IV

Relation between growth along radii with and those without competition with other trees.

Section	Radii	Competition Description	Growth	Radii	Description No Competition	Growth
38-2	1	18" <i>Quercus velutina</i> 27' away	281.25 mm.	6	equidistant between radii 3 and 4	335.5 mm.
	2	6" <i>Carya glabra</i> 18' away	246.75 mm.	7	equidistant between radii 4 and 5	329.50 mm.
	3	16" <i>Nyssa sylvatica</i> 16' away	265.50 mm.	8	equally divide the distance between	285.00 mm.
				9	radii 5 and 1	277.50 mm.
				10		262.00 mm.
	4	23" <i>Q. velutina</i> 22' away	330.50 mm.	11		286.00 mm.
38-3	5	26" <i>Q. velutina</i> 9' away	320.25 mm.			
	Average		284.85 mm.	Average		
	1	24" <i>Q. velutina</i> 16' away	355.00 mm.	5	equidistant between 1 and 3	295.75 mm.
	2	10" <i>Q. montana</i> 24' away	333.00 mm.	6	equidistant between 2 and 3	357.00 mm.
	3	27" <i>Q. velutina</i> 9' away	389.00 mm.	9	equidistant between 1 and 2	303.00 mm.
38-4	Average		359.00 mm.	10		400.00 mm.
	1	26" <i>Q. velutina</i> 4' away	280.00 mm.	4	equidistant between 1 and 2	360.09 mm.
	2	16" <i>Q. velutina</i> 23' away	286.75 mm.	8		425.00 mm.
	3	16" <i>Q. velutina</i> 31' away	322.25 mm.	Average		366.00 mm.
				13	30 degrees from 1	368.83 mm.
				4	15 degrees from 3	292.75 mm.
					equidistant between 4 and 13	324.25 mm.
				6		260.25 mm.



TABLE IV—(Continued)

Section	Radii Average	Competition Description	Growth	Radii Average	No Competition Description	Growth
38-5	1	11" Q. montana	296.33 mm.		30 degrees from 1;	292.42 mm.
	2	30' away	466.50 mm.	11	between 1 and 6	467.75 mm.
	3	9" Q. montana	447.00 mm.	10	38 degrees from 6;	397.75 mm.
	4	7' away	401.75 mm.	7	between 1 and 6	329.75 mm.
	6	7" Q. montana	336.50 mm.	8	35 degrees from 3;	309.50 mm.
		15' away	255.00 mm.	5	between 3 and 4	360.50 mm.
		12" Q. montana		9	37 degrees from 6;	291.75 mm.
		18' away			between 4 and 6	359.41 mm.
		16" Q. velutina			40 degrees from 4;	
		25' away			between 4 and 6	
	Average		361.35 mm.	Average		

TABLE VI

Comparing growth along radii in each cardinal direction of the compass. Radii varied up to 20 degrees either way from any particular cardinal direction.

Section	North			East			South			West		
	Number of Radii	Average Growth	Number of Radii	Average Growth	Number of Radii	Average Growth	Number of Radii	Average Growth	Number of Radii	Average Growth	Number of Radii	Average Growth
38-2	2	300.50 mm.	3	311.58 mm.	1	262.00 mm.	1	281.25 mm.				
38-3	2	330.00 mm.	3	351.33 mm.	2	381.00 mm.	2	391.00 mm.				
38-4	3	286.50 mm.	1	221.00 mm.	1	260.25 mm.	2	313.12 mm.				
38-5	2	467.12 mm.	1	255.00 mm.	2	309.41 mm.	1	329.75 mm.				

TABLE V

Showing relation of slope to unsymmetrical growth

Section	Up-hill side			Down-hill side		
	Number Spreading	Number Radii	Average Growth	Number Spreading	Number Radii	Average Growth
	Roots	Counted		Roots	Counted	
38-2	1	5	278.35 mm.	2	5	365.60 mm.
38-3	2	5	379.80 mm.	2	6	356.50 mm.
38-4	2	7	288.96 mm.	2	7	277.93 mm.
38-5	2	6	381.83 mm.	1	5	346.55 mm.

# A COMPARATIVE POLLEN ANALYSIS OF TWO BOGS WITHIN<sup>1</sup> BOUNDARIES OF THE LATE WISCONSIN GLACIATION IN INDIANA

By BYRON W. MOSS

The study of the migration and succession of forest types by means of fossil pollen analysis is very significant in determining the climatic conditions which have existed since Pleistocene times. Vegetation in its largest aspect is controlled by climate, any gradations of climate are then indicated by the succession of plant types. Pollen spectra derived from analyses of peat are some of the best concrete evidence of vegetational and climatic changes since Pleistocene times.

Loon Lake bog is located approximately four miles west of the town of Silver Lake, in the southwest corner of Kosciusko county. Altona bog is located two miles northwest of Altona in the southwest corner of Dekalb county. The two bogs are separated by about 40 miles in an east-west direction and 20 miles in a north-south direction.

## METHODS

Peat samples from both bogs were obtained during the winter of 1936-7. The peat borer used was of the cylindrical type as described in former pollen studies by Prettyman (8). Samples of peat were taken at each foot-level from the surface to the bottom of the bog. The staining technique approximated that developed by Geisler (4), but the method of mounting the stained material was different throughout. A small amount of the solution was evenly distributed on a clean slide over an area of about 20 mm square. The slides were placed on a level surface and permitted to dry. After the alcohol had evaporated thoroughly the material was covered with a thin coat of sirtillac (12). No cover glass is necessary since sirtillac dries in 24 to 48 hours forming a smooth, hard, transparent surface. Slides made with this medium are permanent and will not discolor with age. To make observations more readily limited to the 20 mm square area, each slide was lined with a razor blade on all four sides to indicate the boundary of the material covered by sirtillac.

<sup>1</sup>This is a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts in Butler University.



These lines are as easy to detect under the microscope as the edge of a cover glass. Pollen grains mounted by this method all occur in the same plane thus very little change in focus of the microscope is necessary to locate all grains and the possibility of overlooking pollen grains which are located at various levels in a medium such as glycerine-jelly is eliminated.

Two hundred grains were counted for each foot-level, except at the surface, the 1-foot layer and the bottom marl levels, where only 100 grains were counted because of low pollen frequency. Barkely (1) concluded that little or no increase in validity accrues from counting above 200 pollen grains per foot-level. At least two slides were used in counting each foot-level, but more were necessary in some cases.

## OBSERVATIONS

The results of the analysis of the Altona bog are presented by stippled bars in figure 1. The bottom level, the only marl level in the Altona bog is characterized by *Abies* and *Pinus*, the former genus being dominant for the marl level only and going out of the spectrum very early. *Pinus* dominated the 22-foot level only but extended to the surface in low percentages. *Picea* did not occur in the marl layer but came into the 22-foot level very strongly and diminished rapidly with a few grains still present near the surface layer. *Acer* shared the dominance of the 17-, 18-, and 19-foot levels with *Quercus* but from there to the surface the latter genus controlled the spectrum by more than 60% per foot-level. *Carya* held a secondary dominance extending from the 14-foot level to the surface. *Salix*, *Tilia*, *Juglans* and *Betula* were persistent in low percentages throughout the spectrum, however none of the broad-leaved genera were found in the marl level.

The results of the analysis of the Loon Lake bog are shown by solid bars in figure 1. The deposits in the lower 5 feet are composed of coarse marl, the remaining levels being made up largely of disintegrated sphagnum. Two layers of peat so dilute that samples could not be taken occurred in the bog, one at the 8-foot level; the other at the 17-20-foot level. Loon Lake bog had 5 feet of marl compared to 1 foot in the Altona bog.

The lowest 6 feet of Loon Lake bog were characterized by *Abies* and *Picea* which dominated all other species. *Abies* was the dominant genus for the lowest 6 feet but disappeared abruptly at the 33-

foot level, while *Picea* remained in low percentages to near the surface of the bog. *Pinus* came into the spectrum at the 38-foot level and dominated all other genera in the 32-, 33- and 34-foot levels after which it gradually decreased in percentage but persisted to the surface. *Quercus* appeared at the 36-foot level and assumed dominance in the 31-foot level, reaching as much as 77.5% at the 5-foot level. *Carya* was secondary in importance. It made its appearance in the 31-foot level and continued to the surface. *Acer* and *Juglans* occurred in low percentages throughout the spectrum except for the marl levels where only the coniferous types were found. *Alnus*, *Betula*, *Salix* and *Tilia* were represented by low percentages in nearly every level except in the marl.

## DISCUSSION

### SIGNIFICANCE OF POLLEN STUDY

In spite of the valuable concrete information gained from records of pollen deposits, there are certainly great dangers of reading too much or too little into some of the percentages obtained. The differences in the amount of pollen produced by various genera, the variability in preservation of pollen, the present difficulty of separating the pollens into species, especially in the case of *Quercus* and *Acer*, the lack of absolute knowledge as to the history of the formation of the physical constituents of the various bogs, i. e. whether the age of the two bogs in the same general geographical location is the same, all add difficulties to the interpretation. Yet in its gross features, a pollen spectrum is one of the most important visible proofs of vegetational changes especially as far as shifts in formations are concerned. In its gross features the vegetation of a given area is the expression of the climatic factors which exist in the area. Changes in genera in a pollen profile of a bog thus, give evidence of the climatic changes which have occurred during the formation of the successive layers of the bog. Clements (3) has shown that plants are the most immediately responsive to climatic influences and constitute the best indication of climatic changes.

However, a pollen spectrum cannot well indicate how much of the vegetational shifting was due to changes in macroclimate and how much was induced by microclimate or by changes in topography. This, no doubt, accounts for the apparent non-correlation between several bogs where pine dominated while the other shows pine of





secondary importance. Soil types and soil moisture select forest types, e. g. in our north-central states pine controls in sandy soil while *Fagus-Acer* or *Quercus-Carya* dominate in areas with better soils. Kell (6) reports for Itasca Park, Minnesota that "water-balance becomes a critical factor in determining the distribution of the major forest types." This water balance is seriously affected by soil texture. Thus, one is no doubt justified to assume that the pine dominance in the 34-, 33-, 32-foot levels in the Loon Lake bog and its absence in every level of the Altona bog is evidently an indication of a soil difference rather than of a difference in macroclimate.

Succession of vegetation may not only be the result of changes in climate, but also in physiographic conditions of an area. Climatic changes cause the greatest variation in vegetation, but within a given area physiographic differences may support more than one type of dominant vegetation. Succession as defined by Weaver and Clements (15) is only a series of progressive reactions by which communities are selected out in such a way that only one survives which is in entire harmony with the climate. Reaction is thus the keynote to all succession, for it furnishes the explanation of all the orderly progression by stages and the increasing stabilization which produces a climax. Succession of dominant forest types as indicated by a pollen profile gives evidence of a northward migration of vegetation. The coniferous forest which dominated all other vegetation in Indiana when the lowermost levels of all Indiana bogs were forming, now is dominating the forests of northern Canada. The complete change from a coniferous climax forest to a deciduous climax forest can be explained by only one factor, viz. climate. Temperature has changed in Indiana from one which favored a coniferous forest, to one favoring the deciduous climax forest now present.

Of significant importance in a study of this kind is the depth to which borings are made. It is perfectly obvious that a spectrum would be incomplete if the boring were incomplete, i. e. if it did not extend to the original lake bottom. In Indiana this is always a sand and gravel layer. If a spectrum is incomplete, the inferences as to succession are naturally incorrect. In all Indiana bogs the transition from a coniferous to a deciduous forest is sudden, i. e. within the range of one foot-level. (See figure 1: Loon Lake bog, levels 37 to 36 and Altona bog, levels 23 to 22.) If a single foot-level were omitted at a critical depth, the impression would be gained that *Quercus*, *Betula* and other broad-leaved species constituted a part of the

forest complex from the very beginning of deposition. Such an error seems to be indicated in Houdek's (5) paper on a bog from Steuben County, which is only 20 miles north of the Altona bog. He shows no *Abies* or *Abies-Picea* climax with absence of all broad-leaved genera which is so characteristic for all Indiana bogs studied in our laboratory. It is quite evident that here in Indiana the boring must be made into and through the hard marl layer if a true picture of forest succession is to be gained. Houdek reports an ooze bottom layer similar to that usually found directly above marl and with pine as the dominant genus and *Quercus* in high percentages.

#### ALTONA BOG AND CLIMATIC CHANGES

In the Altona bog a coniferous forest of *Abies*, *Pinus* and *Picea* dominated the bottom two layers but suddenly disappeared and dominance was assumed by *Quercus* which continued to the surface in high percentages. According to Sears (11) a coniferous forest of this type is an indication of a cool moist climate. The transition from that climate was quite abrupt since *Quercus* with more than 70% dominates all other genera in the third foot-level from the bottom.

Comparing the spectrum of this bog with that of other Indiana bogs, an unusual feature is the high percentage of *Acer* pollen in the 16-, 17-, 18-, 19-foot levels which, when present in other bogs, occurs much closer to the surface. If one takes into account the limited amount of pollen produced by *Acer* as compared with *Quercus*, the percentages of *Acer* pollen in the Altona bog indicate that the abundance of this genus in the forest complex must have been even more significant than the percentage figures indicate. *Acer* has some species which indicate mesophytism, but if *Acer saccharinum*, *A. rubrum* or *A. spicatum* were involved it could indicate a more hydrophytic habitat which might well be only a sub-climax in a *Quercus-Carya* climatic climax.

The climate of the area must have changed from a cool moist, when the coniferous forest was dominant, to a warm moist, when *Acer* and *Quercus* occurred in about equal percentages, to a warm dry which supported a *Quercus-Carya* climax forest such as we have at present. *Betula*, *Juglans*, *Salix* and *Tilia* may be considered as trees which indicate physiographic changes within a *Quercus-Carya* association. The climatic conditions are not necessarily different from those which are required to support a *Quercus-Carya* climax;

rather, the moisture relation is the determining factor which may result from topographic differences. Neither of these genera were represented by high pollen percentages.

#### LOON LAKE BOG AND SUCCESSION

*Abies* and *Picea* were the only genera represented in the lowest 3 feet of deposit in Loon Lake bog. These genera dominated to the 35-foot level but apparently a warmer and drier climate ushered in their decline and eliminated *Abies* entirely at the time when the 32-foot level was deposited. *Picea* had declined to a mere relict. The *Pinus* dominance in the 34- to 32-foot levels gives credit to the assumption that the climate had become warmer and drier, but it might also indicate influence of physiographic factors, for the sandy or low swampy soil near the bog very likely favored establishment of *Pinus* instead of *Quercus* as one finds in many other Indiana bog records. Such variation in forest types adjacent to lakes may be observed easily in the lakes region of our more northern states. The upper two-thirds of the bog records a typical *Quercus-Carya* forest with a fluctuating admixture of *Acer*. The sparse representation of *Fagus* indicates a dry-warm climate or a warm climate and a swampy habitat.

Voss (14) found that the change from *Abies-Picea* to a deciduous forest is generally abrupt in the Illinois bogs, and the present study shows the same feature present in bogs of northern Indiana. If the successive layers of thickness of the peat deposits is a safe indicator of varying elapses of time, we must conclude that conifers controlled for a comparatively short period, in most cases 10% or less of the total time since the retreat of the ice. *Acer*, *Betula*, *Juglans* and *Salix* which were present in low percentages in nearly all levels except the marl levels, may be regarded as natural invaders in a *Quercus-Carya* climax forest in places where the moisture content is high.

#### COMPARISON OF THE TWO BOGS

The two bogs are similar in the rapid decline of *Picea-Abies* and *Pinus* forests and the subsequent rapid ascendancy and persistence of *Quercus* dominance but they do not agree closely regarding the time of these changes. Maple played a very important role in the Altona bog (19-15-foot levels) but it was less prominent in the Loon Lake bog. This is a variation in the deciduous forest complex which might be controlled by local soil moisture conditions.



*Carya* was a representative component of the forest at both places while *Fagus* was absent at Altona and played a very minor role at Loon Lake. The secondary genera *Tilia*, *Ulmus*, *Salix*, *Juglans* and *Betula* were sparsely represented at both stations. In the upper two-thirds of the two bogs there is a uniformity in the genera and percentages of their pollen. In the Altona bog *Picea* was absent in the lowermost level, this was compensated partly by a higher percentage of *Abies*, and this is not uncommon in a number of Indiana bogs studied. In the Altona bog *Pinus* made a prominent showing in the lowest level (27%) while it did not appear in the spectrum of the Loon Lake bog until the 4th foot-level from the bottom and did not reach a comparable percentage until the 8th foot-level. *Quercus* assumed dominance very much earlier in the Altona bog than in the Loon Lake bog.

Summing up the various features we would say that the apparent early dominance of *Quercus*, the comparatively high percentage of *Pinus* pollen in the lowest level, the appearance of large numbers of broad-leaved genera in the second foot-level, the sudden decline of *Abies* in the second foot-level and of *Picea* in the third foot-level in the Altona bog indicate some difference in formation of the two bogs. Loon Lake bog is of the kettle hole type while the one at Altona is of the river valley type, this may mean that the first had abundant water from its very beginning while the Altona bog was a river and by subsequent damming, either by animals, or physical forces, filled in to lake dimensions after a period during which about 7 or 8 feet of marl and peat had accumulated in the Loon Lake bog.

The record of successional changes from boreal to deciduous forest formations is, of course, the same in both bogs, only the time element is poorly correlated in the two depositions. The succession at Altona is *Abies*-*Pinus* (23-22), to *Picea*-*Pinus*-*Quercus* (22-21), to *Quercus* (20), to *Quercus*-*Acer* (19-14), to *Quercus*-*Carya* (13-1). At Loon Lake bog the succession was *Abies*-*Picea* (41-35), to *Abies*-*Picea*-*Pinus* (34), to *Picea*-*Pinus* (33), to *Pinus*-*Quercus* (32-31), to *Quercus*-*Carya* (30-1), with *Acer* as possible co-dominant at the 25-, 23-, and 4-foot levels.

## SUMMARY

1. This study involves a pollen analysis of Loon Lake bog (Kosciusko county) and Altona bog (DeKalb county).

2. Both bogs are located within the boundaries of the Steuben Morainal Lake region (Late Wisconsin glaciation) and are separated in an east-west direction by approximately 40 miles.

3. Loon Lake bog is of the kettle hole type; Altona bog is of the valley type.

4. Both bogs recorded control by a boreal forest during the time the lower levels of deposits accumulated.

5. The large phases of forest succession correlate well in both bogs, but the time indicated for control by conifers was much shorter in the Altona than Loon Lake bog.

6. This difference in time when conifers controlled the forest in these areas is probably due to a later lake formation or to a slower deposition of marl in the Altona valley area.

7. The upper two-thirds of both bogs were more or less comparable in genera present and in their pollen percentages. The most important dominants were *Quercus* and *Carya*.

8. In the Loon Lake area a period of *Pinus* dominance preceded the *Quercus*-*Carya*-*Acer* period while this phase was absent in the Altona area. This was probably due to soil differences.

9. *Fagus* apparently was not an important component of the forests in the areas concerned here.

10. The order of succession of the Altona bog was: *Abies*-*Pinus*, *Picea*-*Pinus*-*Quercus*, *Quercus*, *Quercus*-*Acer* and *Quercus*-*Carya*.

11. The order of succession of the Loon Lake bog was: *Abies*-*Picea*, *Abies*-*Picea*-*Pinus*, *Pinus*-*Quercus* and *Quercus*-*Carya*.

## ACKNOWLEDGEMENT

The writer expresses his sincere appreciation to Dr. J. E. Potzger for suggestions and supervision of this research, and the critical reading of the manuscript; to Dr. R. C. Friesner for the description and collection records of both bogs; and to the members of the Botany Department of Butler University for collecting the peat samples.

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# A FOSSIL POLLEN STUDY OF TWO NORTHERN INDIANA BOGS

By FRANK A. HAMP

Bogs are very common in the northern part of the United States and Canada and are found as far south as Florida and Louisiana. Indiana, however, is the southern limit of extensive bog formations and is doubly significant and interesting since it has within its borders the remains of limits of southern extensions of three glacial invasions whose depositions have "shingled" the state as three great overlapping topographic features showing bogs in all stages of formation, ranging from open lakes in the northern Late Wisconsin deposition to the complete or filled-in "dead bogs" whose chapter is closed, in the depositions of Early Wisconsin glaciations. The glaciers, particularly those of the Wisconsin glaciation, formed what is commonly termed the "kettle-hole" type of bog in Indiana, and it is in the northern tiers of counties where these bogs are most numerous.

Indiana holds an important position for the study of plant migration as Friesner (4) has so well pointed out, calling it a critical botanical area, for it marks within its boundaries the northern limits of southern species and the southern limits for northern species, thus showing the unusual opportunities offered to study plant migration since Pleistocene times.

The two bogs with which this study deals are: (1) Lakeville bog, located in the north half of section 3 (35 north, 2 east), Union Township, St. Joseph County,, and (2) Round Lake bog, located in the east half of section 8 (32 north, 2 west), California Township, Starke County, Indiana. A list of the present-day plants growing in the vicinity of these two bogs may be had upon request to the Botany Department of Butler University.

## METHODS

At both the Round Lake and Lakeville bogs several borings were made, but only the deepest ones at both bogs were analyzed as to pollen representation. The boring used at Round Lake was made in the boggy margin on the west side of the lake. It is recorded as boring "B" and had a depth of 32 feet. The boring at Lakeville bog is

on the records as boring "A." It was 30 feet in depth. It was near the center of the bog which is north of the gravel road running west from U. S. Road 31 at the railroad crossing on the southern edge of the town of Lakeville 0.3 mile west of Road 31.

Samples of peat were taken at each foot-level. The borer was the same one described previously by workers in the Butler laboratories. Geisler's (5) method of separation of pollen from the peat again proved satisfactory. Staining was with aqueous gentian violet. The amount of stain required for good results varied with layers of marl and peat. In some instances 8 drops had to be added to give sufficient stain to the pollen grains. A drop of the finely divided material was placed on a slide and the alcohol was left to evaporate. After it had dried, a coating of sirtillac\* was made over the top of it. Sirtillac does not fog even when 95% alcohol is still present; it clears well and forms a hard, smooth cover which makes the slide permanent without a cover glass. With a razor blade, the surface was scratched in the form of a square cover glass. This aided the investigator in recognizing the edges of the mount.

For all levels, except the lowest two in each bog, 200 pollen grains were counted. In these lowest two levels only 100 grains were counted because of the low frequency in the marl deposits.

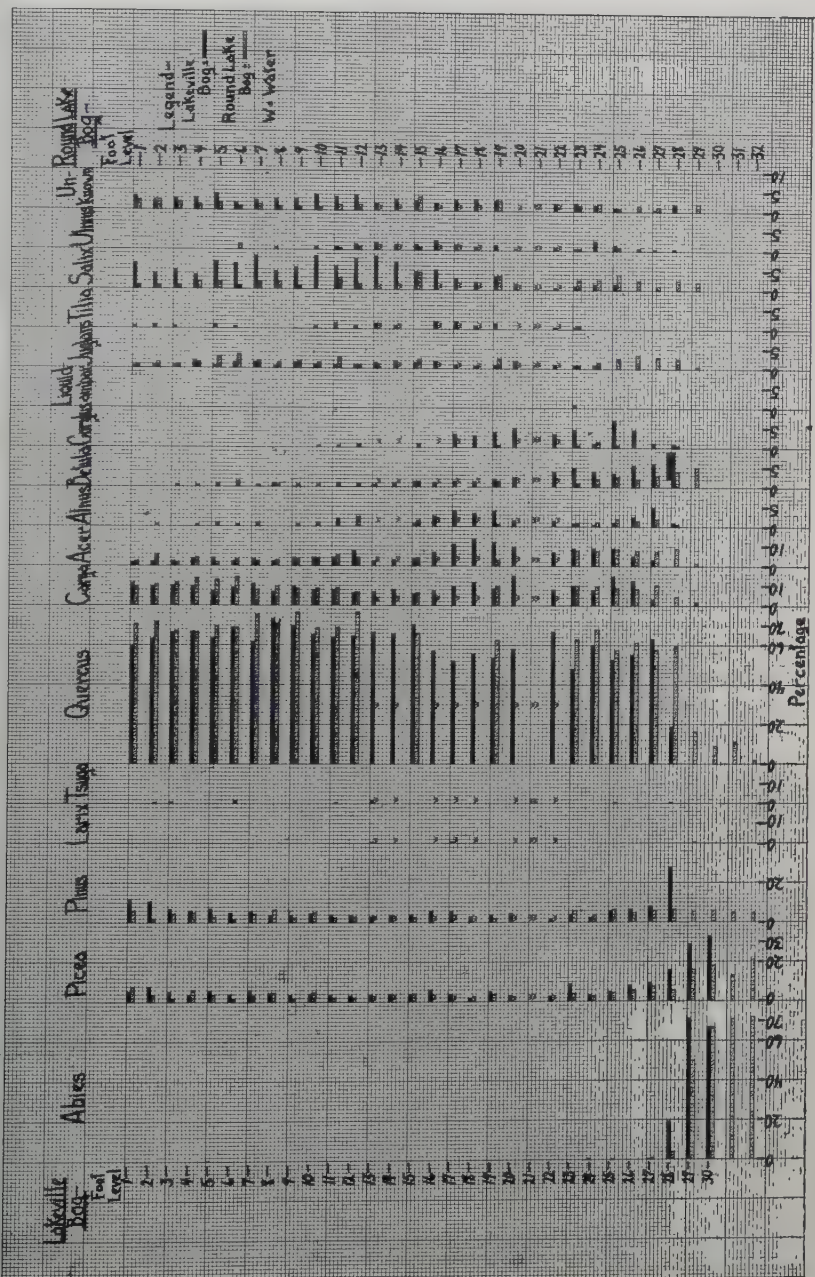
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\*Sirtillac is a new mounting marketed by the Microtechnique Shop, Route 16, Box 698, Indianapolis, Indiana.

## OBSERVATIONS

Of the 32 feet of deposit in Round Lake bog, the 13-, 14-, 16-, 17-, 18-, 20-, 21-, and 22-foot levels were too unconsolidated to permit the opening of the borer and cutting of samples. The lowest two foot-levels were fairly compact marl and these were overlain by three feet of marly ooze. In the Lakeville bog, samples were taken at every level except the 21-foot level. This bog had only one foot of marl and the total depth was 30 feet.

In the Lakeville bog the lowest two foot-levels showed a *Picea-Abies* climax, *Abies* being present in 67% and 71% and *Picea* in 33% and 29% respectively (solid lines in figure 1). An abrupt change occurred in the 28-foot level. *Abies* and *Picea* declined and *Pinus* took over the control, while *Quercus* and *Betula* assumed some importance and *Tsuga* made its appearance. *Abies* continued to decline rapidly from 19% in the 28-foot level to 0.5% in the 27-foot level; *Picea* declined to 9.5% in the 27-foot level but persisted in





small percentages to the surface layer; and *Pinus* declined from the 28-foot to the 27-foot level, but it likewise persisted to the top layer, where it was still represented by 11.5%. *Quercus* gained prominence in the 27-foot level with 63.5% frequency, and *Carya* and *Acer* made their appearance. *Quercus* retained a uniform high percentage to the surface layer.

The *Betulaceae* were represented only about halfway up in this bog. *Alnus* was present up to the 15-foot level, *Corylus* to the 17-foot level, and *Betula* to the 13-foot level with 2 pollen grains present in the 8-foot level. The percentage frequencies were low for all three genera. *Salix* appeared in the 25-foot level, and continued to the top of the bog, reaching a maximum frequency of 8.5% in the 10- and 13-foot levels, and a minimum of .5% in the 22-foot level. *Juglans* pollen was deposited in the bog from the 24-foot level to the surface with percentages never exceeding 2 for any one level. *Liquidambar* was found only at the 23-foot level. *Larix* showed sparse representation. Small percentages of *Ulmus* were present from the 28-foot level to the 8-foot level with the exception of the 9- and 26-foot levels. *Tilia* was represented in all levels from the 23-foot level to the surface excepting 7, 8, 9, 15, and 20.

Boring B, Round Lake, presents a somewhat different spectrum. Here the lowest level had not only *Abies* and *Picea*, as in the Lakeville bog, but also *Pinus* and 2% *Quercus*. In the *Abies-Picea* climax, *Abies* had more than a three to one dominance over *Picea* in the lowest three levels. *Pinus* was represented by a 5% frequency in the 32-foot level, and continued to the surface of the bog never reaching more than a 6.5% frequency.

*Quercus* increased from 2% in the 32-foot level, to 11, 2, 16.5, and 59.5% in the 31-, 30-, 29-, and 28-foot levels, respectively, and continued to the surface with a marked high frequency. It was dominant over all other genera above the 28-foot level with percentages running as high as 77, in the 3-foot level, and 76.5 in the 9- and 12-foot levels.

Although *Abies* persisted only to the 25-foot level, *Picea* continued to the top of the bog, but was no longer a vital factor in the climax above the 29-foot level. The 29-foot level shows a definite climatic change, for here *Larix*, *Acer*, *Betula*, *Carya*, *Juglans*, and *Salix* made their appearance, though in very low percentages. *Alnus* was found in small percentages from the 28- to the 2-foot level, *Betula* to the 3-, and *Corylus* to the 10-foot levels, with all percent-

ages for the entire family not reaching more than 5% for any one genus. Only one *Larix* pollen grain was found in the entire spectrum, i. e. at the 25-foot level, while *Tsuga* pollen was found in several levels of the bog. As previously mentioned, *Acer* and *Carya* both came in at the 29-foot level, and pollen grains of these two genera were found in all succeeding layers. In the upper levels, *Carya* pollen frequency ran considerably higher than that for *Acer*. *Ulmus* was found in the 6-, 11-, 12-, 15-, 23-, 25-, and 26-foot levels, but never running higher than 1.5%. The pollen frequency of this genus was considerably lower here than in the Lakeville bog spectrum.

Figure I represents a graphic presentation of the pollen frequency percentages of the two bogs, the Lakeville bog being shown by the solid line and Round Lake bog by the stippled line.

## DISCUSSION

### LAKEVILLE BOG

The dominance of these, *Abies* and *Picea*, in the lowermost two levels agrees with findings of Sears (14), Potzger (11), Voss (17), McCulloch (7), who worked in various North-Central states, and other investigators who worked peat deposits here in Indiana. Auer (1) found the same condition existing in peat bogs of southeastern Canada.

The loss of dominance by *Abies* and *Picea* and the appearance of such genera as *Tsuga*, *Ulmus*, *Corylus* and *Alnus* indicate a definite change from a cold, moist climate to one that was somewhat warmer. The appearance of such new genera as *Acer* and *Carya* in the pollen spectrum at the 27-foot level, indicate that the climate continued to become warmer, and decrease of *Acer* in all levels from 16 indicates increasing dryness. Especially significant is the increase of *Quercus* from 19 to 63.5%, while *Pinus*, *Picea*, and *Abies* declined strikingly to insignificance. While *Pinus* and *Picea* both continue to the surface of the bog, *Quercus* is the dominant to the top layer of the spectrum, with percentages as high as 70. Similarly high percentages of *Quercus* pollen were found by Potzger (10) in Winona Lake, Indiana deposits. *Pinus* reached its maximum frequency of 27.5% in the 28-foot level. In a way *Pinus* and *Quercus* represent similar climate except that *Pinus* indicates a more sandy soil. Apparently *Pinus* did not control very long anywhere in Indiana. Otto, (8)

found *Pinus* the dominant genus in the 12-foot level of boring IV, Bacon's Swamp, Marion county, Indiana, while Smith (16) reported finding *Pinus* the dominant genus from the 26- to the 22-foot levels of Lake Cicott bog, Cass county, Indiana. *Pinus* was never dominant in other Indiana bogs so far studied (2, 6, 9, 12). In most sections of Indiana the soil adjacent to bogs was of the better clay type and so moderating climate gave *Quercus* a chance to displace *Pinus*. While *Pinus* is recorded in every bog, and is represented uniformly to the topmost layer, it is not consistent in its frequency. At some places it may control while one or several foot-levels were being deposited, while at others it may be represented in the spectrum only by low percentages. A similar correlation is shown between Lakeville bog, and the findings of Sears (15) in an Ohio bog in that there was a definite period when *Pinus* increased immediately following the disappearance of *Abies* and *Picea*, and preceding the rapid increase of *Quercus* and *Carya*.

#### ROUND LAKE BOG

The lower layers of the Round Lake bog differed from those of the Lakeville bog in that *Pinus* and *Quercus* appeared in low percentages in the lowest level, but the climax association was again *Picea-Abies*. *Abies* pollen was represented with a frequency of 72% in comparison to 21% of *Picea*, or more than a 3:1 ratio. In this bog *Pinus* never reached more than 6.5% but was found in all levels, while *Abies* was not represented after the 25-foot level, with the initial decrease being between the 29- and 28-foot levels where a marked drop from 49% in the former level to 4% in the latter was recorded. This extreme decrease marks again a definite climatic change accompanied by a change from the coniferous to the broad-leaved forest, for in this 29-foot level *Quercus* increases to 16% and *Acer*, *Betula*, *Carya*, *Juglans*, and *Salix* enter in very low percentages. In this same level, also, the only *Larix* pollen grain was found. The low frequency is probably due to the fragile and delicate nature of the exine prohibiting a high or normal preservation percentage. In the 28-foot level two other members of the *Betulaceae* appeared, viz. *Corylus* and *Alnus*, and all other genera increased in percentage excepting the genera which had constituted the climax, i. e. *Abies* and *Picea* which continued to decrease. *Quercus* again shows a marked increase, reaching 59.5% and remained high in percentage of pollen present and the dominant genus throughout the remainder of

the bog, in this way being comparable to *Quercus* in the Lakeville bog. While *Carya* came in at the 29-foot level it did not show important percentages until the upper third of the bog, and there could possibly have constituted with *Quercus* a weak *Quercus-Carya* climax. *Tilia* was found only in the 23-foot level, and *Ulmus* and *Tsuga* were present in extremely low frequencies in several foot-levels.

#### COMPARISON OF THE TWO BOGS

While both bogs exhibited a *Picea-Abies* forest climax in the lowest levels, Round Lake bog showed pollen of *Pinus* and *Quercus* in the lowermost level. Since this bog had several feet of marl in the bottom as compared to only slightly over one foot in the Lakeville bog, one would hardly be justified to assume Round Lake bog was not bored deeply enough to show the disappearance of *Pinus* and *Quercus*. Smith (16), Barnett (2), Otto (8), Howell (6), Richards (12), McCulloch (7), and other investigators found *Pinus* pollen in lowest levels, while Prettyman (9), and Sears (14) found this genus appearing at higher levels. This may be explained in part by assuming that after the last glaciation there was a differential northward migration of plants, the migration occurring more rapidly in some localities depending on controlling edaphic and physiographic factors. The earliest period immediately following glaciation was much colder, and deposition within the open lake stage of the bog was slow due to the absence of plants characteristic of our bogs today. These lowermost marl or *Picea-Abies* levels represent many more years deposition than those of higher levels.

Both Round Lake, and Lakeville bogs show the incoming of the deciduous genera at approximately the same levels. This is definite evidence of the aforementioned change in climate, a change from a cold moist to a warmer and somewhat drier climate. While a *Quercus-Carya* climax was dominant throughout the greater part of the bogs above the *Picea-Abies* climax, such sub-dominant genera as *Salix*, *Juglans*, *Acer*, and *Picea*, which were found in every foot-level after making their appearances in the lower levels, show the type of forest indicative of temperatures and forests approaching ours of today.

In Lakeville bog *Tilia* was found in 16 levels while at Round Lake bog only two pollen grains were found. Perhaps the edaphic factors in the neighborhood of Round Lake were not suitable for



growth of *Tilia*, and some pollen grains were blown from some adjoining or nearby suitable habitat area, thus giving a low percentage frequency. *Ulmus* pollen was also found in lesser amounts in Round Lake, showing again the probability of difference in edaphic or other factors. In both bogs *Larix* was sparsely represented, but this may be attributed to the poor preservation qualities of this pollen.

## SUMMARY

1. The paper deals with pollen analyses of Lakeville and Round Lake bogs in deposits of Late Wisconsin glaciation in Indiana.
2. Both bogs have about the same successional record.
3. Succession in the Lakeville bog was: *Abies-Picea* (29-30); *Abies-Pinus-Quercus* (28); *Quercus-Carya* (26-17); *Quercus-Carya-Acer* (16); *Quercus-Carya* (15-1).
4. Succession in the Round Lake bog was: *Abies-Picea* (32-30); *Abies-Picea-Quercus* (29); *Quercus* (28); *Quercus-Carya* (27); *Quercus-Carya-Acer* (26-23); *Quercus-Carya* (19-1).
5. Significant climatic changes from cool-moist to warm-dry are indicated by a striking decrease in *Abies* and *Picea* and appearance of numerous deciduous genera.
6. The Lakeville bog showed a brief *Pinus* dominance in the 28-foot level.
7. *Picea* and *Pinus* persisted to the top foot-level in both bogs.
8. From the 27-foot level in the Round Lake bog and 26-foot level in the Lakeville bog, the forest dominance was essentially *Quercus-Carya* with a weaker co-dominance of *Acer* indicated in several levels.
9. *Quercus* is by far the most important genus in both bogs.
10. *Tsuga* appeared at some levels in very low percentages in both bogs.

## ACKNOWLEDGEMENT

The writer expresses his sincere thanks to Dr. John E. Potzger, who supervised this research, for various suggestions and critical reading of the manuscript; to Dr. Ray C. Friesner for suggestion of the problem, collection and identification of plants in the vicinity of Round Lake, and guidance during the work. The writer also wishes to thank members of the Botany Department of Butler University who aided in the bog boring operations.

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# AN OBSERVATION ON THE EFFECTIVENESS OF ROOT PRESSURE IN THE ASCENT OF SAP

By RAY C. FRIESNER

While making some field observations on stump-sprout reproduction in several species of *Quercus*, a striking exudation of sap from uninjured stems of *Acer rubrum* was noted. After seeing this on a number of specimens, more pointed observations were made with the result that it became apparent that all of the stems showing this exudation through unbroken bark were sprouts from stumps made by logging operations about four years ago. The exudate was coming through the bark of stems ranging from one to two inches in diameter and appeared from six to eight feet above the soil. The volume of sap exuding was sufficient to wet most of the stem below the points of emergence.

These observations called to mind the question of the forces involved in the ascent of sap. Root pressure has always been looked upon as one of these forces but has seldom been assigned a role of any considerable significance. White (Am. Jour. Bot. 25:223-227, 1938) has recently pointed out that the importance of root pressure is probably often underestimated. He found that in the tomato the pressure was in excess of 6 atmospheres and that it may have been as high as 10 atmospheres. It is to be noted that in the present observation on *Acer rubrum* the root system was in every case probably much in excess of that for a normal tree of the same size since the observations were on sprouts from stumps of trees larger than the present stems. While the stumps were not measured, it is estimated that they ranged from 3 to 5 inches in diameter.

Of course, these observations do not mean that the osmotic activity of parenchyma cells along the path of ascent of sap was not involved. These living cells will always exert an osmotic "pull" and this pull may be added to the other forces tending to lift water, but it is difficult to understand how they can exert a "push" as well as a "pull" since a "push" would be necessary for water to leave the ascending path and be "forced" to the outside of the stem through otherwise uninjured and impervious bark.

It is a matter of common observation that sap will exude from broken or otherwise injured points on twigs and stems of *Acer spp.* but these observations differ in that the "bleeding" is through bark unbroken except by the force of the exudate itself. These observations point to the conclusion that turgor pressure is a factor of greater significance than we are prone to allow for it. The fact that we are not able to explain "osmotic push" on any physico-chemical basis does not lessen its importance as a factor in the ascent of sap.



